IV. "On the possibly Dual Origin of the Mammalia." By St. George Mivart, M.D., F.R.S. Received February 14, 1888.

The recent discovery by Mr. Edward B. Poulton of non-functional teeth hidden beneath the bony plates of the jaws of the young Ornithorhynchus is not only most interesting in itself, but taken in connexion with another recent discovery as to the anatomy of that animal, exceedingly suggestive. It is, of course, easy to assign too great a value to the forms of teeth, and everyone knows how Cuvier was thus led to associate the marsupial Carnivora with the placental Carnivores. There is an evident temptation also to exaggerate the significance of dental structure, both on account of the obvious nature of such characters and also because they are so exceptionally well preserved in fossil remains. But no zoologist can deny that the value of dental characters is often exceedingly great, and when, as in the case of *Ornithorhynchus*, we have them in the form of living fossils, as it were, entombed within the jaws, we may fairly presume that they show us what their shape was when they were last in actual use, and so must possess a greater or less taxonomic value. The most valuable evidences of affinity are commonly afforded by structures less distinctly related to habits of life. Thus, for example, the course taken by the internal carotid artery has often a more profound significance than has either the structure of the teeth or shape of the limbs; while the possession by any two animals of a prehensile tail —in spite of the niceties of structure which concur to produce it— cannot alone be accepted as a test that they belong even to the same order.

The shape of the teeth, having a manifest direct relation to conditions of life, requires, then, a very careful criticism before any evidence it may seem to afford can be relied on as a test of affinity.

The *Ornithodelphia* (*Ornithorhynchus* and *Echidna*) have long been known to possess characters resembling the *Sauropsida* and especially the Lacertilian Reptilia. Nevertheless, no less distinguished an anatomist than Professor Huxley has, so late as 1880, regarded them as descendants (through imaginary creatures called *Hypotheria*) from amphibians and not from any of the *Sauropsida*;* a view which I myself have also held.

The most interesting discovery by Mr. Caldwell of the eggs of *Ornithodelphia*, the announcement of which startled the meeting of the British Association in Canada, greatly strengthened the evidence previously relied on by certain naturalists, that the Ornithodelphia descended from some Reptilian form, and this view seems to have

* 'Zool. Soc. Proc.,' 1880, p. 662.

met with general acceptance, and it is similarly supposed that all other mammals must have followed the same route and must therefore also be descendants of some early reptile-like creature.

The question, therefore, of this resemblance or non-resemblance of the Ornithorhynchus teeth with any known reptilian teeth becomes a question of much interest. The author of the recent communication, Mr. Poulton, affirmed that the teeth were distinctly mammalian teeth.*

I have long believed that no such teeth were to be found in any of the Sauropsida, and the conviction I previously entertained has been confirmed by a recent re-examination (*ad hoc*) of the dentition of Reptiles extant and extinct, preserved in the National Collection; and I here desire to express my warm thanks to Mr. G. A. Boulenger and Mr. Lydekker for the very kind and ready help I have received from them.

The results of my examination may be summed up as follows:—

The Sauropsidan tooth, from the lowest reptiles to *Hesperornis*, may be described in general terms as a subconical structure in which subsidiary additions or modifications may arise, which, however, never cause it to resemble a mammalian molar—except, of course, such exceptional mammalian molars as are themselves mere dental cones—or to resemble the mandibular tooth described by Mr. Poulton as existing in *Ornithorhynchus*. That tooth was said to present the following characters:—Towards its outer edge were two large cusps, one in front of the other, and opposite to them were four or five very small ones extending from behind forwards along the inner edge of the tooth. The tooth above it was said to be conversely constructed, so that the two interlocked, the greater prominence of the upper tooth being towards its internal edge.

Nothing of this kind exists in any reptile. In reptiles the dental cone may be laterally compressed and serrated at its margin, as in *Megalosaurus;* it may be less laterally compressed but serrated and furnished with vertical prominences, as in *Iguanodon*. From this we find transitions to the tricuspid tooth of *Cyclura*, and the summit is subdivided into two or three cusps in a multitude of existing lizards, while it may assume the form of a *fleur-de-lys* as in *Amblyrhynchus*. Very rarely (only in *Teius* and *Dicrodon*) there may be a supplementary prominence on one side, which may attain to within a short distance of the height of the main cone and thus present the appearance of a single cone with a deep antero-posteriorly directed groove. Finally, as in *Empedias*† there may be a central prominence

* "The teeth probably represent some part of the molar series in the higher mammals."

† The *Empedocles molaris* of Cope (see 'Amer. Phil. Soc. Proc.,' vol. 19, p. 47). The specimens in our national collection are also thus labelled.

(which appears to become much worn down by use) with a small accessory prominence both on the inner and the outer side of the central one. As every one knows, reptilian teeth may become obtuse rounded structures as in *Cyclodus* and *Ada*, or almost quite flattened as in the curious extinct reptiles *Lepidotus* and *Placodus*. The *Theriodontia** offer examples of teeth more or less like the incisors and canines of mammals, but exhibit no grinding molar, the subdivisions of the summits of their molar teeth sometimes, however, reminding us of the tricuspid molars so common in existing Lacertilians.

Such being the negative evidence with respect to the molar teeth of the Sauropsida, I availed myself of the kind assistance of Mr. Oldfield Thomas, F.Z.S., in an endeavour to find amongst mammals teeth like those described as existing in the Ornithorhynchus. Although various forms were seen to present slight resemblances, we failed to obtain any which could be said to bear an unquestionable likeness to them.

The ancestors of the Ornithorhynchus which had functional teeth, must, according to the ordinarily received doctrine of evolution, have had a general bodily organisation at least as Sauropsidan as that of the existing *Ornithodelphia*. How far back in geological time that tooth structure existed, we have as yet no evidence; but we have abundant evidence that a dentition much like that of some existing Marsupials already existed during the deposition of the Oolite strata. Professor Huxley has expressed† his expectation that generalised ancestors of the Monotremes may be found amongst the remains "of the terrestrial Vertebrates of the later Palæozoic epochs."

The toothed ancestor of the Ornithorhynchus, however, could I think hardly have been extant at so extremely distant an epoch; for then its resemblance in other respects to the *Lacertilia* would make it probable that it had a pretty close connexion with the stem of the Sauropsidan tribe. But a connexion so low down seems unlikely, now that we are acquainted with its tooth-structure; since amongst the multitude of numerous Sauropsidan species living and extinct, there is not one which has inherited a tooth at all like that of the Ornithorhynchus, but the teeth of every one such species is, as above stated, formed upon a fundamentally different type; this could hardly be the case if the Ornithorhynchus tooth was derived from some archaic form whence the Sauropsida, or any considerable section of them, were also derived. But this tooth if not derived from a non-mammalian animal, must either have been derived from some one amongst the

* See Owen's 'Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the British Museum,' 1876, p. 15.

† 'Zool. Soc. Proc.,' 1880, p. 658.

earliest mammals which first had teeth of the mammalian type, or have arisen independently.

Let us first briefly consider the former alternative; such a mammalian ancestor must, on the generally received doctrine of evolution, have had its general organisation like that of an existing Monotreme, or have been formed on a yet lower type. In either case if all mammals furnished with grinding teeth have also proceeded from such early root form, it is remarkable that none of its descendants save the Monotremes have inherited those skeletal, cerebral and genito-urinary peculiarities which characterise the *Ornithodelphia*, and which, on this hypothesis, must also have been possessed by the various ancestors of the different orders of non-monotrematous mammals. In that case, the creatures which came to form all these orders must have simultaneously and persistently varied in a single direction, resulting in that one very definite form of organisation which is common to the placental and marsupial mammals. But this will probably be considered an all but utterly inadmissible supposition.

If, however, the Ornithorhynchus tooth arose in some much less primitive mammal, one which was previously edentulous or had but Sauropsidan teeth, and therefore was not also the progenitor of all the other mammals with grinding teeth, then such teeth must have twice arisen independently, and there seems, on this view, no reason to repudiate the other alternative, namely, that the Ornithorhynchus teeth might have arisen independently, in relatively modern times, in what may have been no very remote ancestor of the Ornithorhynchus itself. In that case, however, the wonder remains that the Monotremes should have retained so many Sauropsida-like features which all other mammals have entirely lost.

The question then presents itself, is it possible that the Monotremes may be instances of degradation; that they inherit their teeth from early but ordinary toothed mammals, while their shoulder-structure, rudimentary corpus callosum, and genito-urinary peculiarities are due to degradation and reversion? It is now considered by some naturalists that the *Amphioxus* and the *Tunicates* are extremely degraded Vertebrates.

When we recall to mind such instances amongst the Invertebrata as *Lerneocera* and *Sacculina*, any amount of degradation seems possible. As to the corpus callosum, considerable differences exist amongst the Placentalia, and it is difficult to see why it might not sometimes shrink as well as augment, and we must admit that the optic chiasma has disappeared in Teleostean fishes, if they had, as would be generally admitted, either Ganoid-like or Elasmobranch-like ancestors. A cloaca is absent in mammals which are not Monotremes, yet such a structure, though very shallow, has reappeared in Rodents and Edentates (Beaver and Sloth). The penis is strangely modified, but the pro-

duction of the mouth of the cloaca of the female eft, *Euproctus*, into an intromittent organ is also startling, and even amongst mammals, the female of the spotted hyæna with its enormous clitoris, perforated by the urethra, is wonderfully different from that of the striped hyæna, otherwise so nearly resembling it in structure. The disconnexion of the ureters with the bladder is a very important difference, certainly, but even in placental mammals those ducts shift their position greatly, as may be seen if we compare *Sorex* with *Hyrax*.

Moreover, it must be admitted that if the Monotremes had remote Sauropsidan ancestors (as can hardly, I think, now be questioned) then more or less of epicoracoids, interclavicles, &c., must have been "in their blood," so that reversion is conceivable. Nevertheless, I am far from believing that such a reversion has actually taken place. Granted that degradation frequently occurs, yet it would hardly, I think, get so completely on the old lines again. There is, however, I venture to believe, another less improbable hypothesis which I will now venture to suggest. It is the hypothesis that the Monotremes come from a radically distinct stock from that whence all other mammals proceeded; that the Monotremes are an example of hypothetical higher mammals in the making, the future evolution of which may probably be hindered by man's presence, but which, did they appear, would produce mammalian forms more or less parallel to but, of course, radically distinct from, the placental and marsupial series of mammals. The latter series of mammals—the superior mammals—may still be supposed to have arisen from Amphibia-like root forms, according to the position defended by Professor Huxley, for which I think there is a great deal to be said. The Monotremes, or inferior mammals, on the other hand, must, I think, be supposed to be derived from Sauropsidan ancestors, and according to this view the resemblances which exist between these higher and lower kinds of mammals, including tooth structure, will be induced resemblances—the two groups having grown alike through the independent origin of similar structures.

What evidence is there that the *Amphioxus* is a degraded animal? What principle of evolution need hinder us from regarding it as a possible parent of another line of Vertebrates profoundly different from the Vertebrates which have come into being? Each of these suppositions is alike hypothetical, and a number of similar dilemmas may be suggested in cases more or less parallel.

With regard to the Monotremes, however, we have a very solid reason for regarding them as mammals which have arisen from another root from the higher (placental and marsupial) Mammalia, namely, the fundamental difference which, according to Professor Gegenbaur, exists between their mammary glands and the mammary glands of

other mammals,* the one being formed from modified sweat glands, and the other from sebaceous follicles. If this distinction is found to hold good throughout the class, it seems to me difficult to think that the Mammalia had not this dual origin—an hypothesis which harmonises so well with the differences, skeletal, genito-urinary, and developmental, which divide these two groups of mammals.

On this view, the teeth of the toothed Ornithorhynchus ancestor must have arisen for the first time in a form more reptilian than is the form of our living Monotremes, yet sufficiently divergent from the Sauropsidan main stem to explain the non-existence of teeth of the kind in any known Sauropsidan, living or fossil.

To this hypothesis it will probably be at once objected, that Mr. Caldwell's† studies of the mammalian ova show a noteworthy resemblance between those of the Marsupials and Monotremes. But if the Marsupials are an offshoot from the placental mammals, then such resemblances as exist between them and Monotremes in this respect must be induced resemblances. Moreover, certain very noteworthy resemblances exist between the ova of those exceptional Amphibians, the *Ophiomorpha*, and Sauropsidan ova.‡ It may be objected in the second place that the dual hypothesis implies the independent origin of too many similar structures. But the independent origin of similar structures is a doctrine for which I have combated ever since the year 1869. I say "similar," not "identical." No two leaves in a forest are *absolutely* alike; how then could absolute resemblance be thought possible between two structures of different origin? Yet the closeness of resemblances between parts which must have arisen diversely is often remarkable. The Marsupials are now regarded as having diverged from the mammalian stem by some single remote ancestor. Yet amongst its descendants have arisen animals some of the teeth of which strikingly resemble some of the teeth of beasts of the placental series. Some teeth of *Perameles* and *Urotrichus*, of *Macropus* and *Macroscelides*, of *Thylacinus* and of *Canis*, may be cited as examples; and though the histological difference of the extension of dentinal tubes into the enamel generally obtains in the Marsupials, yet it is more marked in the Kangaroos, which are the most differentiated forms, while such tubes almost or quite vanish in the *Dasyuridæ*, which more nearly resemble ordinary mammals. But the most striking similarity of tooth structure is that between *Orycteropus* and *Myliobates*—a similarity which extends over the microscopic characters. Again, it would be difficult to find a more curious practical resemblance than that between the hinge teeth of *Lophius*, the

* See his 'Zur Kenntniss der Mammarorgane der Monotremen,' 1886.

† 'Phil. Trans.,' B, vol. 178 (1887) p. 463.

‡ See the account of the ova of *Ichthyophis glutinosus* in C. and P. Sarasin's 'Ergebnisse Naturwiss Forschungen auf Ceylon,' vol. 2, 1887, p. 11.

Pike, and certain fishes yet undescribed. The poison fangs of Serpents have also arisen independently, as is certain when we compare the fang of *Atractaspis* with that of *Vipera*; quite independently also have arisen the poison teeth of *Heloderma*. The scrotum of placentals and the singularly placed scrotum of marsupials (so difficult to explain either by "natural" or "sexual" selection) must also have had a dual origin, as the prehensile pes of *Didelphys* and of the Apes has also doubtless had. For my own part I am still disposed to maintain the probability, which I long ago asserted, of the independent origin of the *Simiadæ* and the *Cebidæ*, and now Professor Cope brings forward* noteworthy reasons for believing that the Horse of America and the Horse of Europe have had a widely distinct ancestry, and have grown alike from two distinct lines of descent. Finally I would refer to the similar forms of placenta, both umbilical and allantoic, which seem to have arisen independently, as also have the mammary glands of Monotremes and other mammals. Any one who is disposed to think incredible the independent origin of a mammalian molar in a diverging offshoot from the Sauropsidan tree, I would ask to bear in mind the multitude of origins which we must regard as independent, and often as quite geologically modern. Among them I would enumerate the dentition of *Desmodus*, *Diphylla*, and *Cheiromys*, and especially the very remarkable multicuspidate canines of a Pteropine bat (*Pteralopex atrata*) recently described† by Mr. Oldfield Thomas. What again can be more singular than the wonderful dental divergence between the Narwhall and the Beluga, otherwise so extremely alike in structure? The poison teeth and, as we shall soon learn, the poison gland and ducts of *Heloderma*, before referred to, are also most noteworthy. Again, what is more startling than to find the respiratory tail of the young *Hylodes* and the respiratory ventral folds of *Rana opisthodon*?‡ The tip of the snout of the young of this animal reminds us of the beak of the unhatched chick, though there can be doubt but that these structures have arisen independently. The development of this Batrachian recalls to mind the similarity of condition of the Axolotl, the larvæ of *Triton alpestris*, and the so-called Perennibranchiate Batrachians, all of which seem to have acquired a normal or permanent condition of life resembling that of immature stages in the existence of their several ancestors.

Mr. Boulenger has been kind enough to inform me of another case of the sudden origin of a new character—probably a reversion—which he has noticed in a Lizard, a species of *Gymnophthalmus*. Here normally the tail is clothed with scales, quincuncially disposed, as in the

* See 'American Naturalist' for December, 1887.

† See 'Ann. Mag. Nat. Hist.,' vol. 1, 1888, p. 155.

‡ See Mr. Boulenger's paper on the reptiles and batrachians of the Solomon Islands, 'Zool. Soc. Trans.,' vol. 12, p. 51.

Scincs. When the tail has been broken, however, it is reproduced with an investment of scales arranged in a verticillate manner—a change which shows how small is the real value of a difference which has been deemed by morphologists to be so important a taxonomic character. And here I would venture to make another observation bearing upon taxonomy. The study of the processes of individual development are of course of great importance in determining the nature of the adult animal. Nevertheless that importance may be exaggerated. *Rana opisthodon* is no less a *Rana* because it is never a Tadpole. The outcome of the process of development is surely as important as the process itself. Similarly with respect to the evolution of species, the lines of descent are of the highest interest, but if Professor Cope is right as to the diverse ancestry of the oriental and occidental *Equus*, then surely its importance may be exaggerated also. The genus *Equus* is no less one genus for having arrived at maturity along two distinct routes. It seems to me probable that various other natural groups, which are commonly regarded, and I think truly regarded, as natural unities, have become one from various sources. Should this view become generally recognised, it seems to me that the idea of the tree of life will not serve as a basis of a really satisfactory system of classification. Certainly no system could be regarded as satisfactory or natural which placed in widely different groups the two kinds of Horse referred to.

In concluding, I beg leave to repeat my assertion, that all the teeth of the Ornithorhynchus are unlike any known Sauropsidan teeth, while nevertheless the totality of the structure of Monotremes, and especially the nature of their mammary gland, lend support to the hypothesis that they have become mammals along a different road from that which the higher Mammalia have travelled, and that they gained their teeth by the way, after they had separated off from the main Reptilian stem. This difference of origin nevertheless constitutes in my eyes no reason whatever for not regarding Monotremes and higher Mammals as being all true members of the one class Mammalia.

Presents, February 16, 1888.

Transactions.

Bologna:—Reale Accademia delle Scienze. Memorie. Ser. 4. Tomo VII. 4to. *Bologna* 1886. The Academy.

Heidelberg:—Universität. Inaugural-Dissertationen, &c., 1887. 8vo. and 4to. *Heidelberg, &c.* The University.

Kiel:—Universität. Inaugural-Dissertationen, &c., 1887. 8vo. and 4to. *Kiel.* The University.

London:—Institution of Mechanical Engineers. Proceedings. 1887. No. 4. 8vo. *London.* The Institution.